RELATION BETWEEN SEXUAL AND ASEXUAL REPRODUCTION IN FRESHWATER BRYOZOA

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RELATION BETWEEN SEXUAL AND ASEXUAL REPRODUCTION IN FRESHWATER BRYOZOA

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Bryozoa, irrespective of marine or freshwater, are colonial and produce new individuals by asexual budding, but they also produce larvae by sexual reproduction. In the order Gymnolaemata (mostly marine forms), various grades of sexual reproduction from oviparity to ovoviviparity are known. The form of the larva and the duration of the free swimming period vary with these grades. In the order Phylactolaemata (freshwater forms), only viviparity is known. The embryo develops in the ooecium, and the digestive tract of the larva is entirely degenerated. The buds are formed within the developing embryo. These facts indicate that asexual reproduction is pushed backwards to the embryonic stage.

Besides sexual reproduction, freshwater bryozoans reproduce asexually by the germinable bodies, *i.e.*, statoblasts and hibernacula. Statoblasts occur in Phylactolaemata, while hibernacula are formed in a limited number of species of Gymnolaemata. These germinable bodies, because of being protected by chitinous envelopes, can survive the intense change of the environment.

However, the relation between sexual and asexual reproduction in freshwater bryozoans has not been studied exactly. In the present paper this relation will be discussed using as material *Lophopodella carteri* occurring in the Furutone Marsh near the Tone River.

1. Sexual reproduction in *Lophopodella carteri*

The larva of *Lophopodella capensis* was first described by Hastings (1929). As to *Lophopodella carteri*, though various studies were made by a number of workers, such as Hyatt (1868), Oka, A. (1907), Takahashi (1934), Rogick (1934, 1935, 1937, 1938) and Toriumi (1941a,b, 1942), the description of the sexual reproduction in this species had not been given until 1948. In that year H. Oka and Oda reported for the first time that ovary and testis develop in *Lophopodella carteri*, and larvae are released from the ooecium. A few words will be added on the sexual reproduction of this species which has been observed since 1948.

The testis is formed on the funiculus and bunches like grapes. The surface of the matured testis is covered with innumerable fine hairs moving slowly with the blood stream. Each hair is the tail of the matured spermatozoon. Well-developed testes were observed in colonies collected in middle July to August. During this period a large part of the funiculus is occupied by the testis. Testis and the rudiments of the statoblasts are often found on the same funiculus. In such a case the testis is formed at the upper part of the funiculus, *i.e.*, nearer to the stomach, while the rudiments of the statoblasts are formed at the lower part of the funiculus.

If a colony with matured testes is laid on a glass plate, the polypides invaginate one by one and the blood flows out through the vestibular pores which are situated on the anal side of the invaginated fold of the cystid. It is then easy to observe under a microscope the free spermatozoa flown out with the blood (Oda, 1958). A matured spermatozoon is approximately 90 μ in length.

The ovary is situated on the cystid wall of the oral side. It is a club-shaped outgrowth of the internal lining epithelium. As shown in Fig. 1, right, several ova in different stages of development are found in the ovary. There remain some problems to be solved as to the mechanism of fertilization.

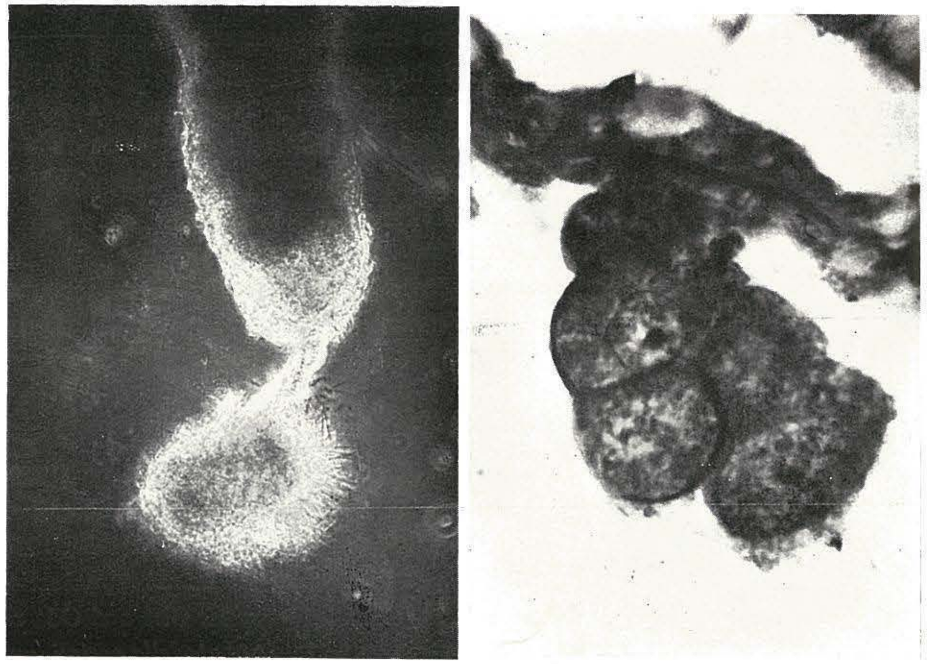

Fig. 1. Gonads of *Lophopodella carteri*.
Left : The testis on the funiculus. *ca.* ×100
Right : The ovary with ova in different stages of development. *ca.* ×750

Developing ooecia were observed in colonies collected during late July to August and a number of larvae appeared from such colonies. Some ooecia and larvae could be observed as late as the middle of September (*cf.* Fig. 4). The ooecium with the embryo, which in the early stage is club-shaped, attaches to the inside of the body wall between cystids. Generally, the embryo is composed of two sections, the germinal part and the outer sac. The ring-shaped buds can be recognized at the upper part of the embryo, *i.e.*, the germinal part. When the embryo develops into a gourd-shape, periodical contraction appears near the rim of the outer sac, *i.e.*, the ring fold. The wave of the contraction extends to both ends of the embryo. This contractive movement occurs at regular intervals. The embryo grows and its shape become pyriform. Finally, it takes an oval shape. During this period buds in the embryo, two in number, gradually develop into small polypides. At the same time the ring fold moves to the upper part of the embryo, as the outer sac extends and covers the germinal part, and the intervals of the contractive movement become shorter. The ooecium with the full-grown embryo stands vertically against the body wall and pushes out the body wall slightly. The embryo rotates occasionally before being released. Finally, that part of the body wall which bears the ooecium opens, and the embryo is released as larva. At that time, the wall of the ooecium is everted and comes out (Oka, H. and Oda, 1948).

The larva is oval or pyriform and is 1.5–0.9 mm in diameter. The larva has usually two well-grown buds, in which the rudiments of tentacles and parts of the digestive tract are clearly distinguished. Exceptionally, the number of buds is one, three or four.

Generally, the majority of larvae appears in the morning, but some of them come out in the afternoon. The larva floats or drifts rotating by means of the cilia on the outer sac. Usually, the oral pole of the larva faces the bottom. Sometimes, the larva is oriented horizontally and moves spirally with the aboral pole forward, but soon returns abruptly to the vertical position and floats again. After floating for a few hours, the larva sticks with the aboral pole to an object nearby and begins to metamorphose. At first the outer ciliated sac, *i.e.*, the larval covering, ruptures at the oral pole and the

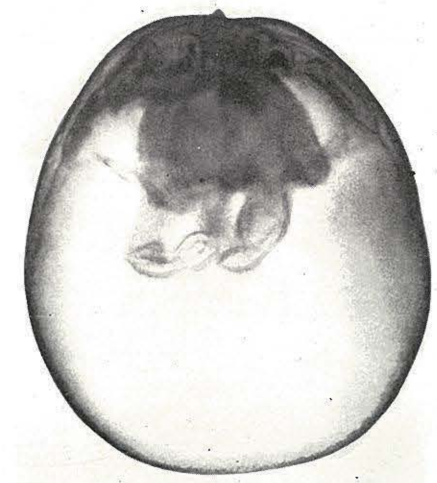

Fig. 2. Larva of *Lophopodella carteri*. *ca.* ×50

concealed body known as the daughter cystid comes out. After that, the young polypides emerge from the daughter cystid one by one. On the other hand, the larval covering shrinks slowly with its rim become slightly evaginated. The tissue of the larval covering becomes light yellowish-orange in color and degenerates. The degenerated larval covering remains as a mass of tissue at the base of the small colony just metamorphosed. Later, this tissue mass separates from the body wall and circulates with the blood stream. Finally, it beraks down into small fragments and is absorbed. The wall of the ooecium everted at the time of the evacuation of the larva also shrinks and degenerates after a few hours.

2. Mode of formation of a colony

The process of germination of the statoblasts in *Lophopodella carteri* has been described in detail (Rogick, 1935, Oda, 1959). In this species only one primary polypide emerges from the statoblast. As the primary polypide grows, two buds at somewhat different stages develop on the oral side of its cystid. The buds emerge and become young polypides. With further budding, the number of polypides rapidly increases.

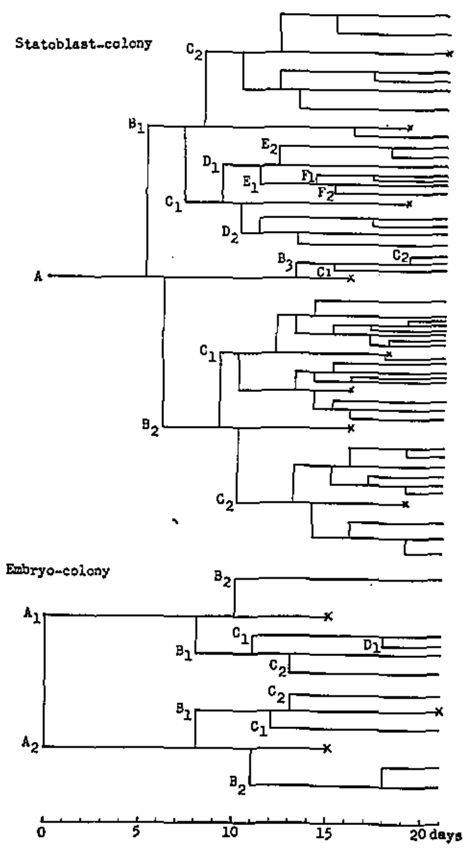

Fig. 3. Mode of formation of a colony in *Lophopodella carteri*.

Now, a colony developed from a statoblast will be called "statoblast-colony". The mode of budding in such a colony is shown at the upper part of Fig. 3. Two types, left and right, of budding are distinguished by the site of the first secondary polypide, and the left type is more common than the right type. A colony grows up regularly by budding of either type. However, in some cases the third bud developes exceptionally late.

In the case of sexual reproduction, the animal after the metamorphoses is already a colony consisting of two young polypides. Later on, a couple of buds is formed in each zooid and these buds develop into young polypides. A colony developed

from a larva will be called "embryo-colony". The mode of budding in an embryo-colony is shown at the lower part of Fig. 3. Both types, left and right, of budding are also found for each primary polypide. So, four combinations of types are distinguished in the mode of formation of an embryo-colony. However, the relative frequency of the four combinations has not been studied.

The well-grown colonies are divided into some pieces, when groups of polypides move to different directions. The number of colonies increases according as the growth of colonies becomes vigorous under favorable conditions. A number of statoblasts are then formed in the body cavities.

3. Relation between the dormancy of the statoblasts and the sexual reproduction

Generally, colonies of *Lophopodella carteri* degenerate in winter with cold, but their statoblasts survive and tide over the winter. The statoblasts kept in the laboratory germinate from late March to early April. But in the field colonies cannot be collected till the middle of July. So, it seems that the germination of the statoblasts in the field starts later than that of the statoblasts kept in the room. However, colonies collected since late July are ready to form actively the statoblasts regardless of the prevailing sexual reproduction.

As Oda (1959) reported, immersing in water, keeping at the proper temperature and exposing to light are necessary conditions for the realization of germination in the statoblasts of *Lophopodella carteri*. When the statoblasts formed in late autumn are kept at the proper temperature, they soon germinate even within the body cavity. The statoblasts formed during the summer do not germinate, even if they are kept at the proper temperature. It is, therefore, concluded that the statoblasts formed during summer months are in the dormancy. It is in that season that larvae appear actively and new colonies are produced sexually.

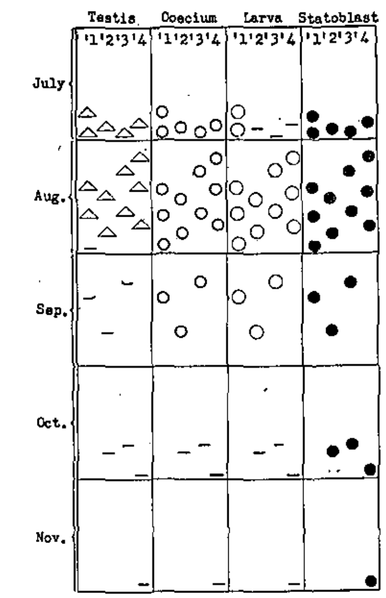

Fig. 4. Relation between the development of the reproductive organs and the formation of the statoblasts in *Lophopodella carteri*. Constructed from the data, from 1951 to 1954.

Some statoblasts, which are formed in the summer and kept under water, can germinate in late September. From this it may be inferred that the dormancy is broken by the decline of temperature. Thus, new colonies are formed asexually from such germinated statoblasts before the following spring. In late autumn the germination of the statoblasts is inhibited by the low temperature.

When the dormant statoblasts are treated with drying or low temperature, their dormancy can be easily broken. So, in the case of a marsh dried out in the summer, the dried statoblasts will soon germinate, if they are given plenty of water again. The statoblasts released in the autumn, on the other hand, if put to the proper temperature, will germinate before the following spring.

As mentioned above, embryo-colonies are actively produced during the season, in which the dormant statoblasts are formed. And the dormant statoblasts acquire germinability, once they are exposed to unfavourable conditions such as drying, low temperature, etc.. Therefore, the statoblasts are significant as a means of reproduction rather than that of hibernation.

Now, larvae of *Pectinatella gelatinosa* have not been found to date, although both reproductive organs, ovary and testis, were observed (Oka, A., 1890, Oka, H. and Oda, 1948). It is probable that the reproduction of this species entirely depends on the statoblasts.

By the way it may be added that we have succeeded in the summer of 1959 in taking a 16 mm motion picture of the different ways of reproduction of *Lophopodella carteri* in co-operation with the Educational Film Department of the Toei Motion Picture Co. Ltd., Tokyo. The film is entitled "Tiny Pond Animals".

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